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*Published in:*  
Journal of Plankton Research

*Link to article, DOI:*  
[10.1093/plankt/fbw094](https://doi.org/10.1093/plankt/fbw094)

*Publication date:*  
2017

*Document Version*  
Peer reviewed version

[Link back to DTU Orbit](#)

*Citation (APA):*  
Mcconville, K., Atkinson, A., Fileman, E. S., Spicer, J. I., & Hirst, A. G. (2017). Disentangling the counteracting effects of water content and carbon mass on zooplankton growth. *Journal of Plankton Research*, 39(2), 246-256. <https://doi.org/10.1093/plankt/fbw094>

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# Disentangling the counteracting effects of water content and carbon mass on zooplankton growth

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Keywords; water content, zooplankton, gelatinous, carbon percentage, growth

26

27 *ABSTRACT*

28 Zooplankton vary widely in carbon percentage (carbon mass as a percentage of wet mass), but are  
29 often described as either gelatinous or non-gelatinous. Here we update datasets of carbon  
30 percentage and growth rate to investigate whether carbon percentage is a continuous trait, and  
31 whether its inclusion improves zooplankton growth models. We found that carbon percentage is  
32 continuous, but that species are not distributed homogeneously along this axis. To assess variability  
33 of this trait in situ, we investigated the distribution of biomass across the range of carbon percentage  
34 for a zooplankton time series at station Plymouth L4. This showed separate biomass peaks for  
35 gelatinous and crustacean taxa, however carbon percentage varied 8 fold within the gelatinous  
36 group. Species with high carbon mass had lower carbon percentage, allowing separation of the  
37 counteracting effects of these two variables on growth rate. Specific growth rates,  $g$  ( $d^{-1}$ ) were  
38 negatively related to carbon percentage and carbon mass, even in the gelatinous taxa alone,  
39 suggesting that the trend is not driven by a categorical difference between these groups. The  
40 addition of carbon percentage doubled the explanatory power of growth models based on mass  
41 alone, demonstrating the benefits of considering carbon percentage as a continuous trait.

42

43 *INTRODUCTION*

44 Gelatinous zooplankton are a phylogenetically broad and ecologically important group of taxa  
45 found throughout the world's oceans. Their prey range from bacteria to fish (Sutherland et al.,  
46 2010) and they exhibit an equally diverse range of life history strategies and body compositions.  
47 The high water content characteristic of this group can be expressed as carbon percentage (carbon  
48 mass as % of wet mass), with some taxa having carbon mass as low as 0.01% of their wet mass  
49 (Clarke et al., 1992; Harbison, 1992; Lucas et al., 2011; Kjørboe, 2013).

50

51 Interest in gelatinous zooplankton is linked to a growing appreciation of their impact on pelagic  
52 ecosystems and human activities (Richardson et al., 2009; Purcell, 2012; Gibbons and Richardson,  
53 2013). For example, the introduction of the ctenophore, *Mnemiopsis leidyi* to the Black Sea has had  
54 considerable financial implications for fisheries in the area (Shiganova and Bulgakova, 2000).  
55 Research on gelatinous zooplankton has grown apace with basic ecological interest in the

physiology, trophic ecology and bloom dynamics of this group (Møller and Riisgård, 2007; Gemmell et al., 2013; Condon et al., 2013).

Based on a compilation of zooplankton body composition, Kiørboe (Kiørboe, 2013) found that most zooplankton species are either gelatinous (~0.5%) or non-gelatinous (5-10%), with comparatively few intermediates. Indeed, much research has been directed toward comparing and contrasting gelatinous versus non-gelatinous zooplankton. For example, compared to other planktonic animals, gelatinous zooplankton have higher carbon mass-specific feeding rates (Hamner et al., 1975; Acuña, 2001; Acuña et al., 2011), lower locomotion costs and higher specific growth rates (Hirst et al., 2003; Pitt et al., 2013). Indeed, gelatinous taxa such as salps are amongst the fastest growing metazoans (Bone, 1998).

The use of a categorical approach to zooplankton body composition (i.e. gelatinous versus non-gelatinous) contrasts with the treatment of carbon mass (Peters, 1983), which is used as a continuous variable in many models of growth (Hansen et al., 1997; Gillooly et al., 2002, Hirst et al. 2003). However, the carbon percentage of zooplankton species also varies widely, even among gelatinous taxa (Molina-Ramirez et al. 2015). A recent review suggested that water content was second only to body size in determining key aspects of the biology of zooplankton (Andersen et al., 2015b). So far, empirical models of zooplankton growth use equations that are specific to various taxonomic groups (e.g. Hirst et al. 2003, Kiørboe & Hirst, 2014) and these equations have not yet been unified. As carbon mass and carbon percentage are both variable traits, it is important to consider them together in empirical models of zooplankton growth. Furthermore, quantifying the relationship between growth rate and carbon percentage may help to explain how carbon percentage functions as an evolutionary trait, and, for example, why there are gelatinous representatives from six phyla found in the plankton.

In this study we have used both a meta-analysis approach and an in-situ time series of zooplankton from weekly sampling at the Plymouth L4 time series (Smyth et al. 2015). We had three objectives. The first was to quantify the degree of variability in carbon percentage both in “trait space” from the meta-analysis dataset and in a natural plankton assemblage, to gauge whether it was appropriate to treat water content as a continuous variable. The second aim was to investigate the degree of collinearity between carbon mass and carbon percentage, again both in a meta-assemblage and in

the L4 assemblage. Dependent on the outcome of these two objectives, the third aim was to construct a simple empirical model of zooplankton growth that combines carbon mass and carbon percentage.

## *METHODS*

### *Carbon percentage data*

Ratios of wet mass to carbon mass were combined from a series of recent compilations (Kjørboe, 2013; Pitt et al., 2013; Molina-Ramirez et al., 2015). The amalgamated dataset with their sources is presented in Supplementary Information 1. Only concurrent measurements of carbon and wet mass of the same individual were used to calculate carbon percentage.

The degree of tissue dilution of zooplankton taxa has been expressed previously as body carbon content (Molina-Ramirez et al., 2015). However to avoid confusion with carbon mass, throughout this paper it is referred to as “carbon percentage” (carbon mass as a percentage of wet mass). For our comparisons the levels of taxonomic organisation were selected based on functional diversity and body form (e.g. phylum for Chaetognatha, but orders Cydippida and Lobata).

### *In situ analysis*

To investigate how species biomass was distributed along the spectrum of carbon percentage in an in situ community, the L4 zooplankton time series (Western Channel Observatory, Plymouth) was used. The L4 sampling site is approximately 15km south-west of Plymouth and undergoes seasonal stratification (Harris, 2010). Sampling at the L4 site consists of a pair of vertical hauls with a 200  $\mu\text{m}$  WP2 zooplankton net from 50 m to the surface (maximum depth 54m). The nets are retrieved at 20  $\text{cm s}^{-1}$  and are immediately fixed in 4% formaldehyde solution (Maud et al., 2015). The zooplankton are then subsampled, counted and identified (Eloire et al. 2010). This zooplankton abundance times series has high resolution both temporally (weekly sampling) and taxonomically, with many taxa consistently identified to species level since 2009. To determine zooplankton biomass, a total of 3780 individuals from the formalin-preserved catches at L4 taken throughout 2014 and 2015 were measured. From standard length measurements (e.g. cnidarian bell height or diameter, copepod prosome length), length-carbon mass relationships from the literature were used to estimate carbon masses per individual. These length measurements were then aggregated into seasons, namely spring (March-May), summer (June-August), autumn (September-November) and

119 winter (December to February) to account for the high intraspecific variability in length observed at  
120 L4 (Atkinson et al., 2015). This allowed us to derive season-specific mean carbon masses per  
121 individual, which were multiplied by numerical densities to estimate biomass density ( $\text{mg C m}^{-3}$ ).  
122 Previously measured, L4-specific seasonal values of individual carbon biomass were used, when  
123 available (e.g. *Calanus helgolandicus*; Pond et al. 1996).

124

125 Of the approximately 189 taxa recorded at L4, only 22 contributed more than 0.5% to the total  
126 biomass for all species. To examine how biomass was distributed across the spectrum of carbon  
127 percentage, these taxa were assigned to  $\log_2$  classes (0.1 - 0.2%, 0.2 – 0.4%, 0.4 – 0.8%, 0.8 – 1.6%,  
128 1.6 – 3.2%, 3.2 – 6.4%, 6.4 – 12.8%, > 12.8%) using the carbon percentage data in Supplementary  
129 Information 1. The distribution of carbon biomass in each carbon percentage category across the  
130 seasons was then calculated.

131

#### 132 *Growth rate data*

133 Using the references from the appendices of Kiørboe and Hirst (Kiørboe and Hirst, 2014) as a  
134 starting point, zooplankton growth rate data were extracted from the original sources and  
135 augmented by searching the literature. All growth rate data used here are in Supplementary  
136 Information 2.

137

138 To improve comparability of source data we restricted the meta-analysis to data from laboratory  
139 incubations with food available in high (assumed non-limiting) concentrations. By using only data  
140 collected under these conditions we suggest that the measurements are more directly comparable,  
141 with the observed patterns more likely to reflect the intrinsic biology of the species than external  
142 factors.

143

144 Published growth rates are normally expressed either as increase in length or body mass over time.  
145 When organism size was expressed as length, published length-mass regressions were used to  
146 convert to body carbon mass (Hirst, 2012; Kiørboe and Hirst, 2014). To express growth rates in the  
147 terms commonly used for zooplankton (as an exponential rate; see Hirst and Forster 2013), the  
148 mass-specific growth rate,  $g$  ( $\text{d}^{-1}$ ) was determined as:

149  $g = (\ln M_t - \ln M_0)/d$

150 where  $M_t$  is mass at time  $t$ ,  $M_0$  is mass at the previous time point, and  $d$  is the time period between  
 151 the two measurements of mass (in days).

152

153 Growth data were temperature-corrected to 15°C using a  $Q_{10}$  of 2.8 (following Hansen et al., 1997;  
 154 Kiørboe and Hirst, 2014). General linear models (GLMs) were constructed in R (R Core Team,  
 155 2014) to determine the relationships between growth rate, carbon percentage and carbon mass. To  
 156 determine whether there was collinearity between the predictor variables we examined the condition  
 157 indices for the variables in the model using the *colldiag* function in the *perturb* package in R  
 158 (Hendrickx, 2012). A condition index of greater than 30 is considered large (Belsley et al., 1980)  
 159 and suggests that the variable should be removed from the model.

160

161 When growth data were available for a species but carbon percentage values were not, the latter was  
 162 estimated using the mean value for the highest level of taxonomic relatedness available. For  
 163 instance, if composition values for a species were not available, then the composition values for all  
 164 other species within the genus were averaged and used as an estimate. The estimates were typically  
 165 at the genus level but no lower relatedness than family (38% estimated at family level, primarily for  
 166 copepods).

167

## 168 *Growth rate analysis*

169 Four analyses were performed; the first two were based on mean and maximum growth rates for all  
 170 zooplankton taxa in the dataset, the second two as above but for the classical gelatinous taxa only  
 171 (Cnidaria, Ctenophora and Thaliacea). Maximum growth values were defined as the highest  
 172 temperature-adjusted growth rate value available for each species. Issues of non-independence  
 173 between data were avoided by using single growth rate values per species per study. For illustrative  
 174 purposes only (i.e. the plots in Fig. 4), we adjusted all growth rates to a fixed body carbon mass of  
 175 1mg C after correcting to 15°C. This mass correction was performed assuming  $\log_{10}$  mass-specific  
 176 growth ( $g$ ) scales against  $\log_{10}$  mass with a slope of -0.25 (Brown et al. 2004).

177

## 178 *RESULTS*

## 179 Variability in carbon percentage across the zooplankton

180 The range in body volume for two animals of equal carbon mass but at either end of the carbon  
 181 percentage spectrum is demonstrated in Figure 1. For the compiled dataset, the range in carbon  
 182 percentage extended over four orders of magnitude in zooplankton, from 0.01% in the lobate  
 183 ctenophore, *Bathycyroe fosteri*, to 19.02% in the copepod, *Calanus hyperboreus* (Fig. 1, 2a,  
 184 Supplementary Information 1). The intervals between adjacent ranked species were small relative  
 185 to the range covered (Fig. 2a), suggesting that water content could be considered as a continuous  
 186 variable. The largest interval between species coincided with the shift from the classic gelatinous  
 187 taxa to other zooplankton (i.e. from Thaliacea to Chaetognatha). However, this difference between  
 188 species constituted a relatively small fraction of the total range (6.8%). In addition, there was  
 189 overlap of classic gelatinous and non-gelatinous groups. For example, some chaetognaths were  
 190 within the traditional gelatinous range (1.27% and 1.35% for *Pseudosagitta lyra* (as *P. scrippsae*)  
 191 and *Pseudosagitta* (as *Sagitta*) *gazellae* respectively), whereas one tunicate had a carbon percentage  
 192 which lay within the non-gelatinous range (3.87% for *Doliolum denticulatum*). This overlap of  
 193 taxonomic groups was extensive across the spectrum of water content, as can be seen by the mixing  
 194 of colour across Fig. 2. This was particularly the case among the Ctenophora and Thaliacea with the  
 195 range of both taxa approaching two orders of magnitude in carbon percentage.

196

197 The wide variation in body carbon percentage observed at a species level in Fig. 1a is also  
 198 summarised at the broader taxon level in Fig. 2b. Median values for groups do loosely cluster into  
 199 gelatinous and non-gelatinous taxa following the bimodal distribution of species suggested by  
 200 Kiørboe (Kiørboe, 2013). The ranges of all adjacent taxa (excluding lobate ctenophores)  
 201 overlapped, with Thaliacea and Chaetognatha bridging the gap between the classical gelatinous and  
 202 non-gelatinous taxa. The variability within groups was greater for gelatinous taxa, with the greatest  
 203 range in the scyphomedusae, closely followed by the thaliaceans. The gelatinous taxa sort into their  
 204 respective phyla when ranked (i.e. Lobata, Nuda, Cydippida for the Ctenophora, then  
 205 Hydromedusae and Scyphomedusae for Cnidaria) suggesting that taxa within phyla are on average  
 206 more similar to each other than with other phyla.

207

208 In the natural assemblage sampled at the Plymouth L4 site (Figure 3) we have an alternative picture,  
 209 namely how biomass is distributed along this spectrum of carbon percentage. At L4, biomass is  
 210 distributed bimodally. The biomass is primarily concentrated in the categories that are either highly



211 gelatinous (carbon mass 0.1 – 0.8% of wet mass) or non-gelatinous (6.4 - > 12.8%) However, there  
 212 is considerable variability within the carbon percentage categories, as some gelatinous taxa are as  
 213 much as 8 times larger in wet mass for the same carbon mass as others. The biomass in the  
 214 intermediate categories (0.8 – 1.6% and 1.6 – 3.2%) was very low and below our threshold for  
 215 inclusion. This area of the spectrum is populated by thaliaceans and large rhizostome  
 216 scyphomedusae, which are either not commonly recorded at L4 (thaliaceans) or are rarely or poorly  
 217 sampled by the 0.57 cm diameter nets used. Gelatinous taxa comprise a greater proportion of  
 218 biomass in summer than the other seasons. In winter, chaetognaths (3.56%) have similar total  
 219 biomass to the dominant copepods. There is also a broad trend of increasing carbon percentage  
 220 through the year within the gelatinous taxa. In spring, the cydippids (the most gelatinous group  
 221 frequently encountered at L4) are dominant, followed by Nuda (Beroe) in summer and finally  
 222 hydromedusae and siphonophores in autumn.

223

#### 224 *Relationship between carbon mass and carbon percentage*

225 There were negative relationships between carbon mass and carbon percentage, both in the meta-  
 226 dataset (Fig. 4a) and in the in situ dataset (Fig.4b). While the more gelatinous taxa tended to have  
 227 higher carbon mass there was considerable variability, with some organisms of similar carbon mass  
 228 differing 100-fold in carbon percentage (Fig. 4). To ensure that collinearity was not influencing the  
 229 growth model the condition indices for the variables were inspected. The highest condition index  
 230 observed was 3.05, lower than the threshold of 30 suggested by Belsley (Belsley et al., 1980)  
 231 confirming that carbon mass and carbon percentage can be used in combination in models of  
 232 zooplankton growth. As gelatinous and small organisms tend to grow fastest, the tendency for more  
 233 gelatinous taxa to have higher carbon mass underlines the need to include both as covariates in our  
 234 growth model.

235

#### 236 *Relationship between carbon percentage and growth rate*

237 We first conducted GLMs on the subset of data comprising the classical gelatinous taxa alone.  
 238 These showed that mean growth rate declined with increasing mass and increasing body carbon  
 239 percentage. The GLMs on the whole dataset established that  $\log_{10}$  mass-specific mean and  
 240 maximum growth rate was significantly correlated with both  $\log_{10}$  carbon mass and  $\log_{10}$  body  
 241 carbon percentage (Fig. 5, Table I). As expected, there was a negative relationship between  $\log_{10}$   
 242 mass-specific growth rate ( $g$ ), and  $\log_{10}$  carbon mass, in line with the results of Kiørboe and Hirst

(Kjørboe and Hirst, 2014). In the analyses of all zooplankton taxa, mean and maximum growth rate decreased with increasing carbon mass and carbon percentage.

245

In all analyses, the addition of body carbon percentage to models of growth based on carbon mass alone increased the explanatory power (Table II). The second order Akaike criterion, AICc, (Burnham and Anderson, 2002) was lower in the model including water content in all analyses, supporting the inclusion of this factor in analyses of zooplankton growth. In the maximum analysis including all taxa, Akaike weights ( $\omega_i$ ) were approximately 10 times higher in the models including body carbon percentage (mass  $\omega_i = 0.08$ , mass + carbon percentage  $\omega_i = 0.92$ ). This suggests that these models were significantly better than models based on mass alone (Royall, 1997). A similar pattern was observed in the analysis of maximum growth rates of the gelatinous taxa however it was not observed for mean growth rates (mass  $\omega_i = 0.02$ , mass + GI  $\omega_i = 0.98$ ).

255

## 256 *DISCUSSION*

Our study provides strong support for: body carbon percentage being a continuous trait, for a negative relationship between body carbon percentage and growth rate, and for considerable increases in model predictive power as a result of inclusion of this trait for zooplankton. Below we discuss the implications of each of these findings in turn.

261

Kjørboe (Kjørboe, 2013) demonstrated that if zooplankton are arranged in a frequency distribution based on body composition, that most taxa are either gelatinous (carbon mass is ~0.5% of wet mass) or non-gelatinous (~5-10%), with little overlap. Our study would appear to contradict this, since we found a fairly continuous distribution of carbon percentage. However, this does not conflict with the findings of Kjørboe (Kjørboe, 2013), since in that study it was emphasised that most taxa are either highly gelatinous or non-gelatinous. Rather, we highlight that, while the most species fall into one of these two groups, there is considerable variability in carbon percentage within each group and there are representatives across much of this spectrum. The distribution of zooplankton biomass at L4 supports both of these views. Biomass is clustered at either end of the spectrum as described previously, and this could suggest that the fitness landscape for this trait favours extremes. However, at either end of the spectrum there is considerable variability. The traditional gelatinous group alone spans an 8-fold range in carbon percentage, with implications for growth rate. For

example, there is a trend of increasing carbon percentage among the gelatinous zooplankton through the year, with cydippids being replaced by beroids in summer and finally by hydromedusae and siphonophores in autumn.

277

In the meta-analysis compilation, the largest interval occurs between taxa typically considered as gelatinous and intermediate, between the pelagic tunicate, *Thalia* (as *Salpa*) *democratica* (1.6 % body carbon percentage) and a chaetognath, *Eukrohnia hamata* (2.7 % body carbon percentage. Molina-Ramirez et al. (Molina-Ramirez et al. 2015) stressed that considerable variation in carbon percentage existed even within the classic gelatinous taxa (Cnidaria, Ctenophora and Tunicata). Our results are in agreement, albeit with even higher degree of variability (at 350-fold). Taken together, the relatively small interval between values for gelatinous and non-gelatinous species and the high variability observed within the gelatinous taxa suggest that growth models can indeed incorporate carbon percentage as a continuous trait.

287

When  $\log_{10}$  mass-specific growth rate was regressed against  $\log_{10}$  body carbon percentage as a continuous variable, a negative relationship was observed. Crucially, the pattern persisted when considering the gelatinous taxa alone (Table II). The existence of the relationship among the gelatinous taxa alone, is important as this demonstrates that the relationship is not due to a categorical difference between gelatinous organisms and non-gelatinous organisms.

293

One potential mechanism that could explain the relationship between body carbon percentage and growth rate is enhanced feeding rate (Acuña et al., 2011). These authors suggested that the large dilute bodies of gelatinous zooplankton facilitate higher carbon-specific feeding rates than other zooplankton taxa of the same carbon mass. If this increased feeding rate drives faster growth, then this might explain the relationship of increasing growth rate with decreasing carbon percentage (see Fig. 2). As many gelatinous taxa are filter or ambush feeders that rely on capture surfaces to feed, assuming that feeding rate scales with surface area, then we may expect the scaling exponent between surface area and body carbon percentage to match the exponent for growth rate and body carbon percentage. To investigate this we used a simple geometric calculation. Assuming isomorphic growth, surface area (SA) scales with body volume with a power of 0.67. By altering degree of gelatinousness for a fixed amount of body carbon, SA then scales with carbon percentage with a power of -0.67. Hence, with an assumption that growth rate is a fixed proportion of feeding

rate, this would give the same slope of -0.67 for  $\log_{10}$  mass-specific growth versus  $\log_{10}$  carbon percentage (Fig. 2). The exponents that we determined empirically across the various zooplankton taxa are less steeply negative than -0.67 (at -0.18 and -0.16 for mean and maximum respectively), i.e. increasingly gelatinous organisms increase their growth rate less rapidly than these surface considerations would predict. This could indicate a potential feeding inefficiency associated with decreasing carbon percentage or that factors additional to surface area may also be important.

In common with Ikeda (Ikeda, 2014), we found that species with larger total carbon masses also tended to be more watery. Furthermore, as the larger organisms are typically more watery the effects of carbon mass and carbon percentage tend to counteract, underscoring the need to include these variables together in order to better predict growth. Molina-Ramirez et al. (Molina-Ramirez et al., 2015) found a similar result for tunicates but found that body carbon percentage was invariant with increasing mass for cnidarians and ctenophores. The authors suggested that this might be due to differences between internal filter feeding in tunicates and external ambush or cruise feeding in the other groups. It has been suggested that feeding modes decrease in efficiency with increasing size (Kjørboe et al. 2011), so high water content may help to mitigate this decrease in efficiency and maintain relatively higher carbon specific feeding rate at large carbon masses. This is supported by the findings of Acuña et al. (Acuña et al., 2011), suggesting that gelatinous plankton had higher carbon-specific feeding rates than other zooplankton of a similar carbon mass. Together with higher growth rates, these factors could help to explain how gelatinous zooplankton are capable of forming such high localised increases in species biomass (blooms).

While the increase in capture surface area and associated feeding and growth rates is one potential advantage of the gelatinous body form, there are other implications. There are potential negative implications also, especially with regard to limited swimming speed and escape responses. While medusae have potential defences in the form of nematocysts, many gelatinous taxa such as ctenophores do not, and may have limited ability to escape from potential predators as a result of their large dilute bodies (Acuña, et al. 2011). Understanding why some taxa are gelatinous is not always straightforward. The most gelatinous mollusc in this analysis is *Clione limacina*, a gymnosome predator that feeds on almost exclusively on *Limacina helicina*. *Clione* does not rely on large capture surfaces or on generating a feeding current as it ambushes individual, relatively large prey items. In this case, water content does not appear to be a derived trait to increase body volume relative to carbon for feeding, suggesting that this may not be the only driver of high water content

in zooplankton. It has been suggested that potential other causes include physical or ecological factors such as transparency to impair visual predation (Hamner et al., 1975) or the efficiency of neutral buoyancy (Kjørboe, 2013). Together these factors may help to explain why semi-gelatinous bodies are observed in at least six major planktonic phyla (Cnidaria, Ctenophora, Chordata, Annelida, Chaetognatha, Mollusca, see Supplementary Information 1).

## CONCLUSIONS

Body size is often described as a master-trait, and is frequently used as the sole intrinsic variable in empirical and simulation models involving zooplankton growth (Kjørboe and Hirst, 2014, Anderson et al., 2015a). But what do we mean by “body size”? Carbon mass is often used as the unit for size, but both our meta-analysis and the real assemblage data show that carbon percentage also varies greatly. It may even vary negatively with carbon mass, leveraging an opposing effect on growth. We argue that carbon mass and carbon percentage are both key traits, both are intrinsic to the zooplankton and since they are possible to estimate, then we should disentangle their separate effects in a unified growth model. By including carbon percentage to models of growth based on carbon mass alone, we substantially increased their explanatory power, with smaller body masses and lower body carbon percentages leading to higher specific growth rates. Building on the work of previous publications (Kjørboe, 2013, Pitt et al., 2013, Molina-Ramirez et al., 2015) we provide a carbon percentage dataset in Supplementary Table 1. By using these source data alongside carbon masses, the maximum growth rate equation in Table 1 may then be used as a starting point to estimate growth rates attainable by zooplankton.

Alongside the “size” based simplifications used for modelling, there has also been an increase in “trait-based” modelling in which categorical variables or functional groups are allowed to vary continuously. A purpose of this paper is to allow water content also to be used as a continuous trait; to facilitate its inclusion alongside carbon mass and other traits such as feeding mode (Litchman 2013; Andersen et al. 2015a; Hébert et al., 2016). Since we found that growth rate depended on carbon percentage even among the gelatinous taxa alone, we hope that considering and modelling water content as a continuous trait will reveal the ecological and evolutionary factors that influence the water content of zooplankton.

## ACKNOWLEDGEMENTS

371 We thank the numerous authors (cited in Supplementary Tables 1 and 2) whose measurements of  
 372 body composition and growth rate have made this meta-analysis possible. We also thank the crew  
 373 of the RV *Plymouth Quest* and to Rachel Harmer and Andrea McEvoy who analysed the  
 374 zooplankton data. We thank Martin Lilley for help with the length-mass conversions of the  
 375 gelatinuous taxa. KM was in receipt of a Natural Environment Research Council National (NERC)  
 376 funded studentship, and was partly funded together with AA, EF and AGH by the NERC and  
 377 Department for Environment, Food and Rural Affairs (grant no. NE/L003279/1, Marine Ecosystems  
 378 Research Program).

379

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## 490 TABLE AND FIGURE LEGENDS:

491 Figure 1. Comparison of the relative carbon (black) and wet masses (grey) of *Calanus hyperboreus*  
 492 (left, carbon percentage = 19.02%) and *Bathycyroe fosteri* (right, carbon percentage = 0.01%). The  
 493 relative area of each shade is scaled as volume so the silhouettes are representative of true size.

494

495 Figure 2. (a) Zooplankton species ranked according to their carbon percentage (CM%WM; log<sub>10</sub>  
 496 scale), each horizontal bar represents a single species. Colours indicate taxonomic groups as  
 497 detailed in the legend. (b) Zooplankton taxonomic groups ranked according to their carbon mass (as  
 498 % of wet mass; log<sub>10</sub> scale). Boxes indicate median, lower and upper quartiles with whiskers  
 499 showing the range. (Vertical lines at 0.5 and 5 CM%WM represent the composition of the  
 500 gelatinous and non-gelatinous taxa defined by Kiørboe 2013).

501

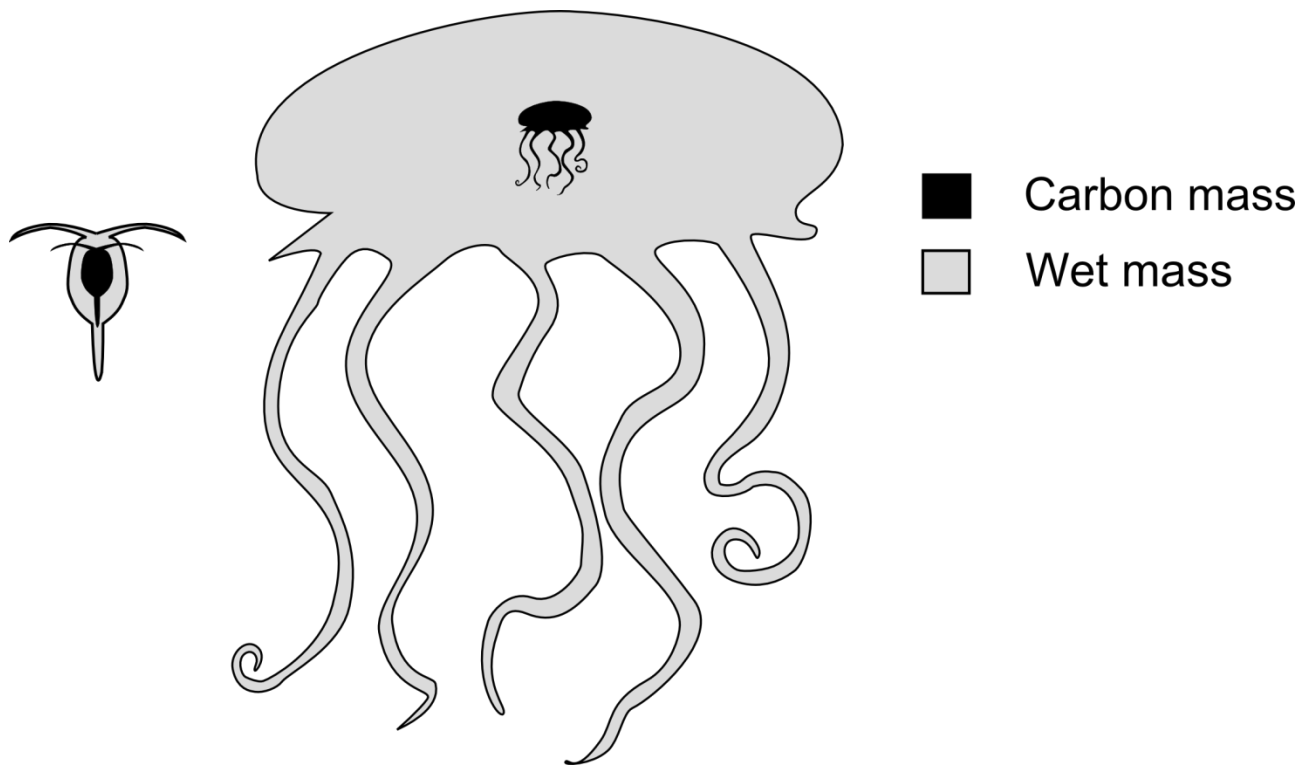
502 Figure 3. Distribution of carbon biomass (mg C m<sup>-3</sup>) between log<sub>2</sub> carbon percentage (CM%WM)  
 503 categories through spring, summer, autumn and winter (2009-2015) at the L4 sampling site,  
 504 Western Channel Observatory, Plymouth. The same colour coding of taxa is used as in Fig. 1 – see  
 505 legend. \* - Biomass value for the category 0.4 – 0.8 exceeds the scale in summer (34.4 mg C m<sup>-3</sup>) as  
 506 a result of 7 high abundance observations of *Beroe spp.* (of total 318 samples). Upper limit of  
 507 biomass scale in winter is 5 mg C m<sup>3</sup>.

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509 Figure 4. Carbon percentage (CM%WM) as a function of carbon mass (mg) for the meta-analysis  
 510 dataset (A, log carbon percentage = - 0.26 \* log carbon mass - 0.18, p = 0.0001, R<sup>2</sup> = 0.21, df = 60)  
 511 and the L4 assemblage (B, log carbon percentage = - 0.34 \* log carbon mass - 1.1, p = 0.0026, R<sup>2</sup> =  
 512 , df = 20). Taxonomic groups coloured as indicated in the legends.

513

514 Figure 5. Specific growth rate,  $g$  ( $d^{-1}$ ) as a function of body carbon percentage (CM%WM). Growth  
515 values were temperature-adjusted to  $15^{\circ}C$ , mass adjusted to 1 mg C and then averaged for each  
516 species in each study. (a) mean mass-specific growth rate values for each species in each study and  
517 (b) maximum specific growth rate values for each species.



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540 Fig 1

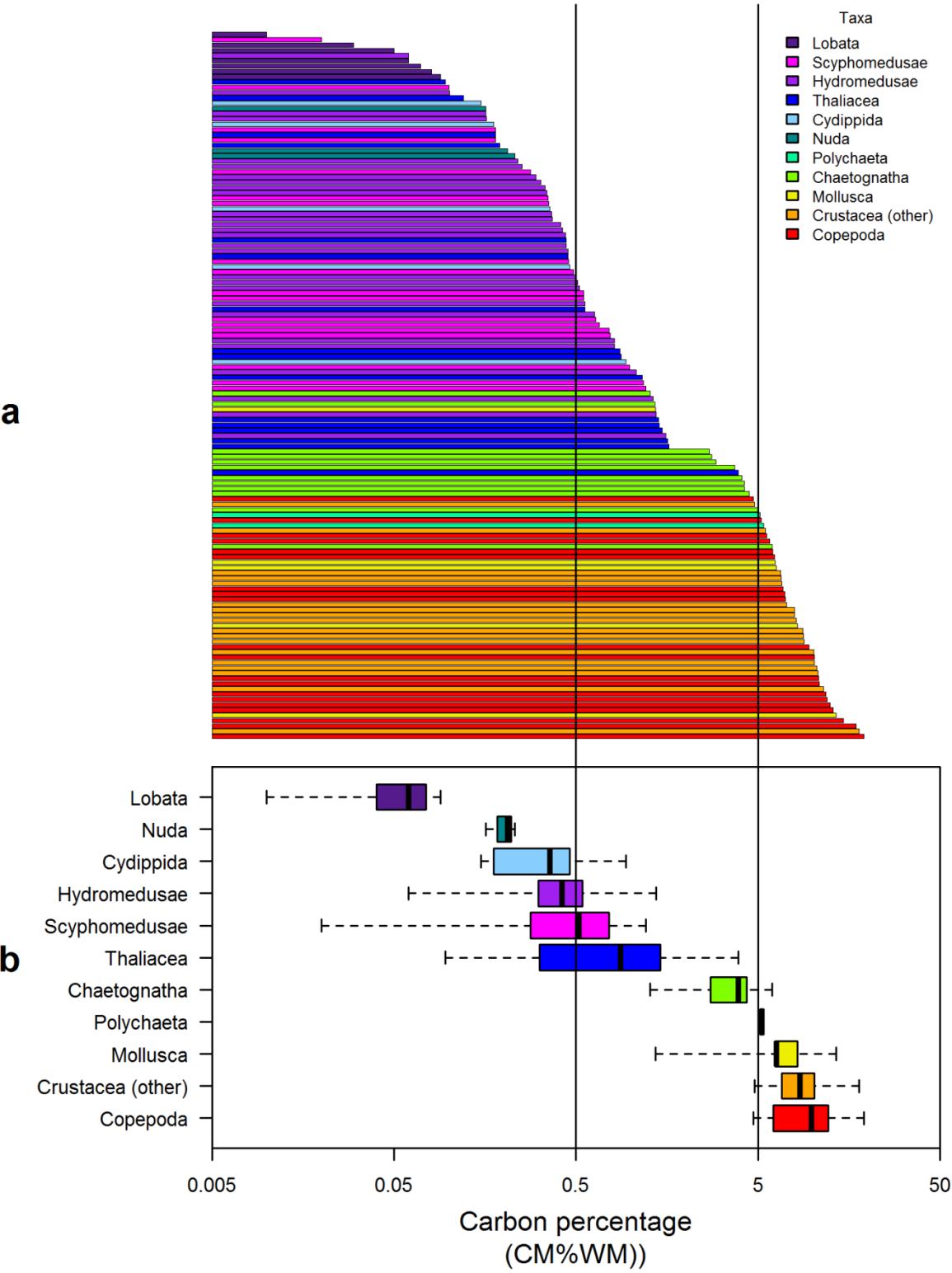
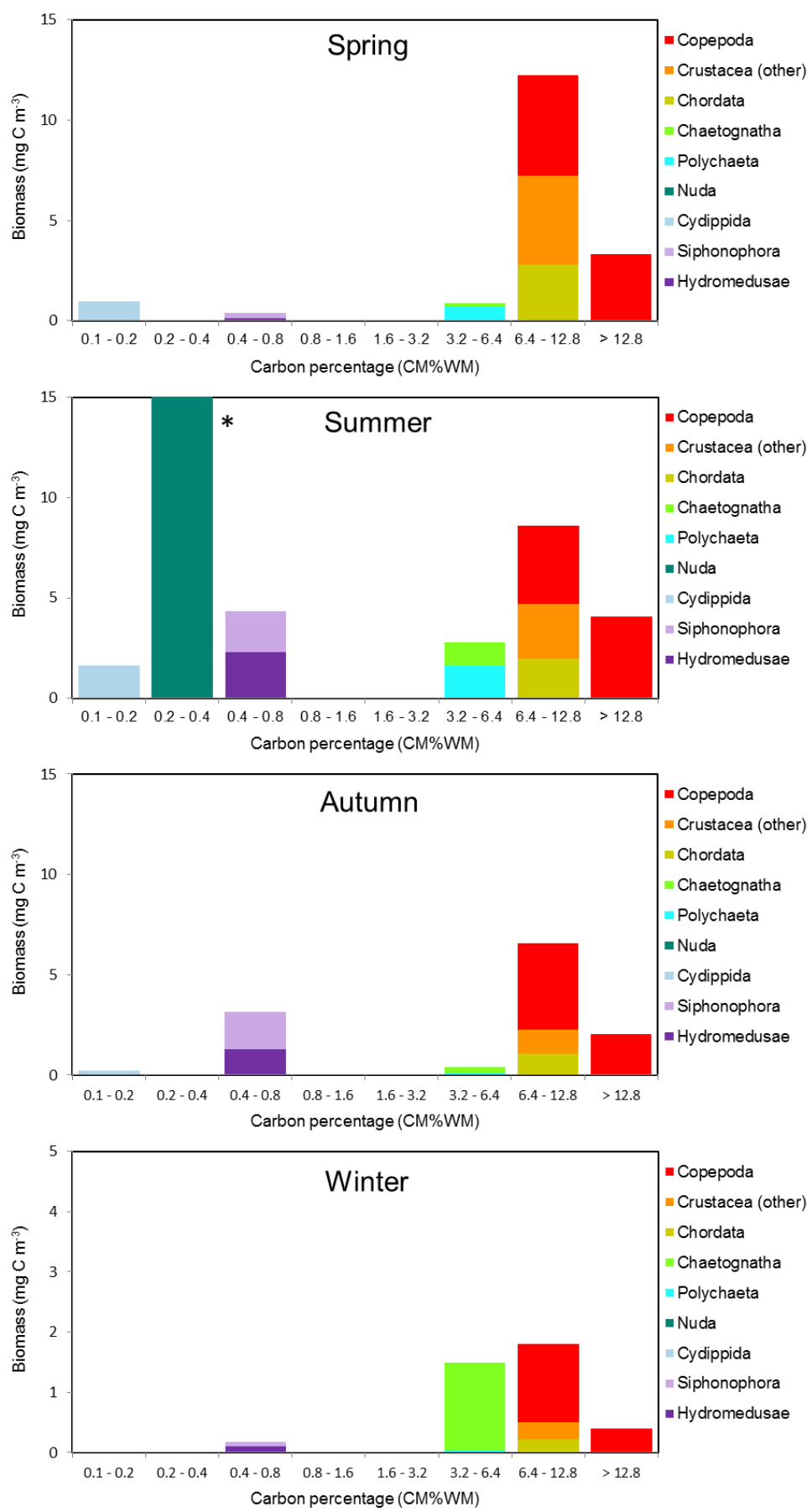


Fig 2



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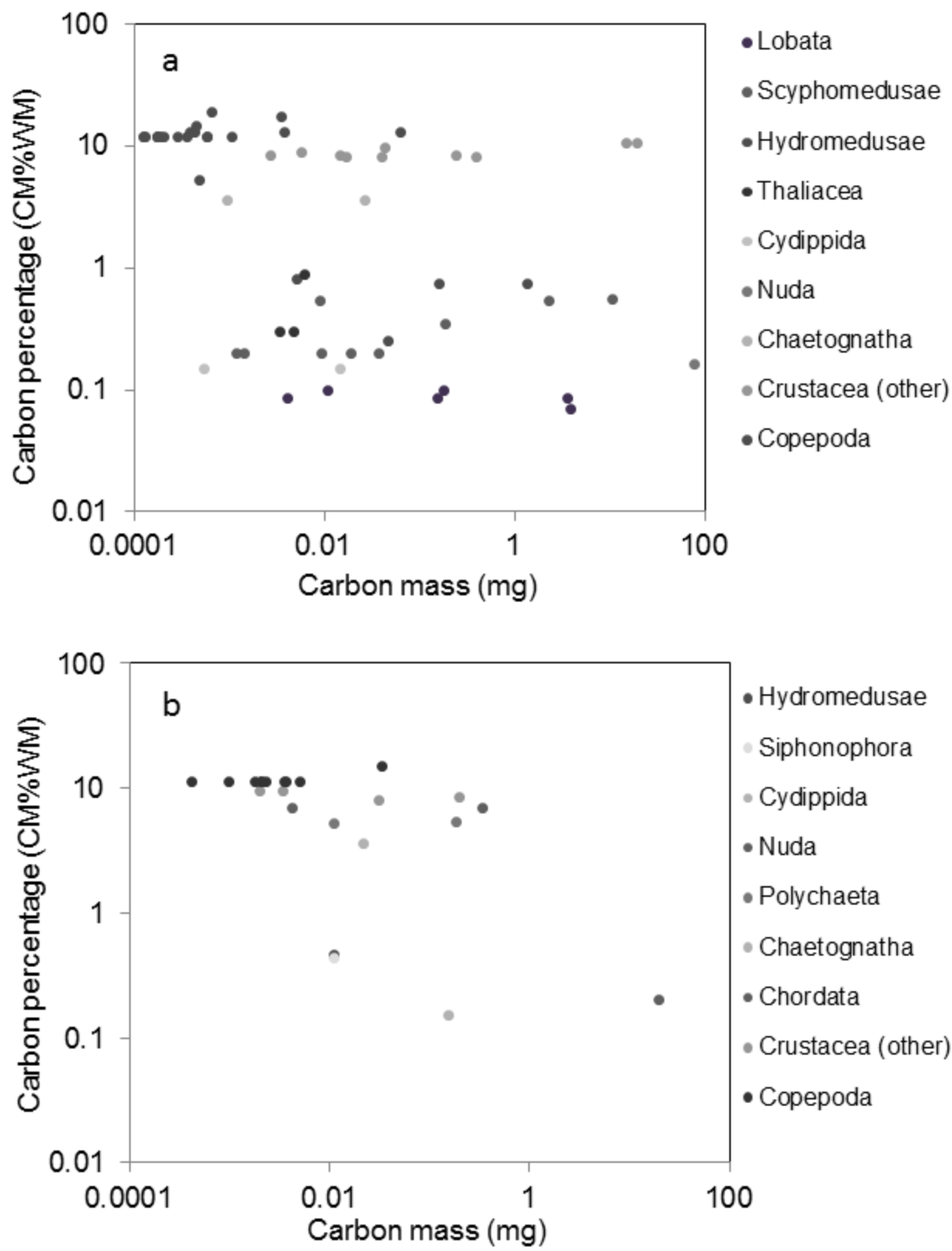
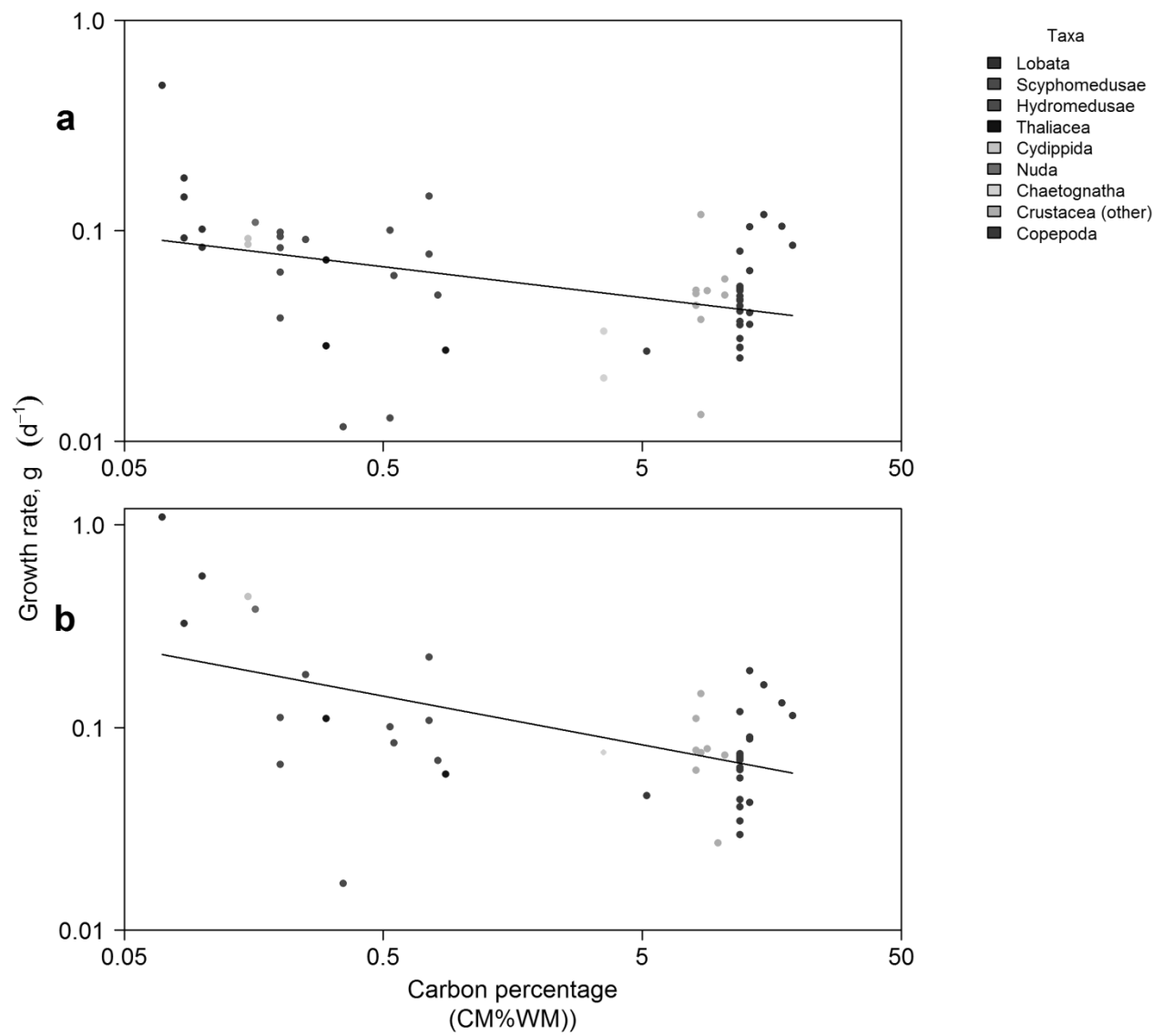


Figure 4





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552 Fig 5

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559 Table I. General linear models predicting  $\log_{10}$  mean specific and  $\log_{10}$  maximum specific growth  
560 rate,  $g$  ( $d^{-1}$ ), as a function of both  $\log_{10}$  carbon mass (mg) and  $\log_{10}$  body carbon percentage  
561 ( $100 \cdot (CM/WM)$ ). All models pertain to growth rate data that were first  $Q_{10}$ -adjusted to  $15^{\circ}C$ .

562

563 Table II. Changes to measures of explanatory power of models of growth based solely on carbon  
564 mass when body carbon percentage (CC) was added as a factor. AICc is the corrected Akaike  
565 information criterion,  $\Delta_i$  is the AIC difference, and  $\omega_i$  is the Akaike weight. Models with Akaike  
566 weight values 10 times greater than that of the other models being compared are considered  
567 statistically significant as optimal models (mass + GI for mean and max all zooplankton and max  
568 gelatinous taxa only). All models pertain to growth data that were first  $Q_{10}$ -adjusted to  $T = 15^{\circ}C$ .

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| Group                |                    | Factor                              | df | <i>p</i> | Slope | Intercept | Adj R <sup>2</sup> |
|----------------------|--------------------|-------------------------------------|----|----------|-------|-----------|--------------------|
| All zooplankton      | Mean growth rate,g | log <sub>10</sub> carbon mass       | 58 | <0.0001  | -0.17 | -1.12     | 0.43               |
|                      |                    | log <sub>10</sub> carbon percentage |    | 0.036    | -0.18 |           |                    |
|                      | max growth rate,g  | log <sub>10</sub> carbon mass       | 42 | <0.0001  | -0.16 | -0.81     | 0.31               |
| Gelatinous taxa only |                    | log <sub>10</sub> carbon percentage |    | 0.013    | -0.16 |           |                    |
|                      | mean growth rate,g | log <sub>10</sub> carbon mass       | 22 | 0.027    | -0.19 | -1.18     | 0.33               |
|                      |                    | log <sub>10</sub> carbon percentage |    | 0.038    | -0.17 |           |                    |
|                      | max growth rate,g  | log <sub>10</sub> carbon mass       | 13 | 0.011    | -0.16 | -1.15     | 0.42               |
|                      |                    | log <sub>10</sub> carbon percentage |    | 0.018    | -0.72 |           |                    |

Table I

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| Group       | <i>g</i> | $R^2$ |           | AICc  |           | $\Delta_i$ | $\omega_i$ |           |
|-------------|----------|-------|-----------|-------|-----------|------------|------------|-----------|
|             |          | Mass  | Mass + CC | Mass  | Mass + CC |            | Mass       | Mass + CC |
| All         | Mean     | 0.39  | 0.43      | 18.63 | 16.67     | 2.47       | 0.19       | 0.81      |
| zooplankton | max      | 0.22  | 0.31      | 21.99 | 17.57     | 4.42       | 0.076      | 0.92      |
| Gelatinous  | mean     | 0.33  | 0.33      | 18.51 | 19.96     | 1.44       | 0.54       | 0.46      |
| taxa only   | max      | 0.09  | 0.42      | 21.55 | 16.26     | 5.29       | 0.019      | 0.98      |

Table II